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Simple Stochastic Populations in Habitats with Bounded, and Varying Carrying Capacities

Master's thesis in Complex Adaptive Systems

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Abstract

A population consisting of one single type of individuals where reproduction is seasonal, and by means of asexual binary-splitting with a probability, which depends on the carrying capacity of the habitat, K and the present population is considered. Current models for such binary-splitting populations do not explicitly capture the concepts of early and late extinctions. A new parameter v, called the 'scaling parameter' is introduced to scale down the splitting probabilities in the first season, and also in subsequent generations in order to properly observe and record early and late extinctions. The modified model is used to estimate the probabilities of early and late extinctions, and the expected time to extinction in two main cases. The first case is for fixed and large K, where a new and more general upper bound for the expected time to extinction is proposed to be e^{vK}. The risk of such populations going extinct is found to be of the order $\mathcal{O}\left(\frac{1}{\sqrt{(2v-1)K}}\right)$. The second case considers a scenario where the carrying capacity of the habitat varies in each season between two values L (for low) and H (for high), randomly chosen with equal probabilities to represent either a good or a bad season respectively. Both cases yielded similar results with the probability of early extinction tending to zero as v increases, and the probability of late extinction tending to one as v increases.

Keywords: habitat; carrying capacity; branching processes; supercritical; subcritical; extinction time; binary-splitting.

Contents

1. Introduction

1.1 Background and Motivation

The marriage between Mathematics and Biology is known to have a very long history, giving birth to a diverse, and vibrant inter-disciplinary research field known today as Mathematical Biology. Mathematical Biology is the umbrella name for research areas such as Theoretical Ecology, Evolutionary Biology (or Population Genetics), Computational Biophysics, and Population Dynamics just to mention, but a few. This project work falls under Population Dynamics, which is the study of the time evolution of the size of the population as well as the factors that affect the growth and development of the population. This helps in addressing questions concerning conservation of endangered species, management of fish and wildlife, and cell and tumour kinetics. In addition, basic knowledge about the processes that affect population dynamics can be used to predict future patterns of human population growth.

Mathematical description of biological systems makes it possible for their behaviour (and or evolution) to be better simulated and studied. This means that properties of the systems that might not be evident to the experimenter can be predicted by using mathematical models. The increasing study of realistic and practically useful mathematical models in Population Dynamics is a reflection of their use in helping to understand the dynamic processes involved, and also in making practical predictions (Murray, 2001). In Population Dynamics, a mathematical model makes it possible to calculate explicitly the values of important population parameters, such as the doubling time or the growth rate, from parameters that describe individual behaviour (Haccou et al., 2005).

Mathematical models used in Population Dynamics are of two kinds: deterministic, and stochastic. Deterministic models are usually formulated in terms of differential equations. Many simple classic formulations of population dynamics, in terms of differential equations, can be used to show that non-ageing individuals have exponentially distributed life span (Haccou et al., 2005). Thomas Malthus in his essay, On the Principle of Populations (Malthus, 1798), asserted that “Population, when unchecked, increases in a geometrical ratio.” This is exactly the characteristic of the famous exponential population growth model, which is formulated as a differential equation. Four decades later in 1838, Pierre-Francois Verhulst published his logistic population growth model. (See Tsoularis (2001); and Bacaer (2011) for detailed description and analysis of the logistic population growth model.) Verhulst derived his logistic growth model to describe the self-limiting growth of a biological population. This was also a deterministic model formulated in terms of a differential equation in which the rate of reproduction (or population growth rate) is proportional to both the current population size and the amount of available resources. The limiting resources were captured in a parameter called the carrying capacity. An analysis of the logistic population growth model shows that the exponential population growth model is a special case, when the population size is small compared to the carrying capacity. Thus the carrying capacity is the limiting value of the population size.

Hence the highest value that the population can reach given infinite time (or come closer to in finite time) is equal to the carrying capacity. Therefore, exponential population growth is not forever.

The deterministic models of population dynamics fail to address the role of randomness in nature, that the fate of individuals is stochastic. Every biological population is influenced by factors such as predation risk, food access, weather, and other factors that can best be described as being random (or stochastic) (Haccou et al., 2005). This means that population size may fluctuate around a stationary point for a very long time. However, these fluctuations are not permanent, and so the ultimate fate of every biological population is extinction. Therefore, appropriate models to address extinction in population biology are those of stochastic nature. Stochastic population growth models treat population growth as a random (or stochastic) process[1] with one absorbing state[2], which is the extinction state. Once the process had reached the extinction state, it never recovers from that state. This imposes some sort of finiteness on the size of biological populations.

The finiteness requirement is essential, in that, natural populations are finite (Klebaner et al., 2011). The place of extinction in population dynamics cannot be understood within the framework of deterministic population models (Haccou et al., 2005). That not withstanding, we can always approximate the deterministic dynamics from the stochastic dynamics, if we allow population size to approach infinity, through some arguments equivalent to that of the law-of-large-numbers. This work therefore mainly seeks to study the properties of simple stochastic populations in habitats with bounded, and varying carrying capacities. The simplest of such conceivable stochastic population growth models is that of asexual binary-splitting populations, in which each individual either divides into two new ones in the next generation (or season) or just dies out (Klebaner et al., 2011). The habitat considered in such a model is assumed to have a *carrying capacity* K. If the present population is of size $Z_n = z$, the probability of an individual successfully splitting into two new ones can be taken as $\frac{K}{K+z}$ in a first simple model, and individuals reproduce independently (Klebaner et al., 2011).

Stochastic population growth models require the study of statistical properties of the population. One tool that has successfully been applied in this regard is branching processes. Branching processes are concerned with probabilistic descriptions of life careers, the basic purpose of which is to deduce properties of populations from probability laws of individual childbearing and life span (Haccou et al., 2005). It is therefore not surprising that many methods and techniques used in population biology have a branching process background or interpretation, and so it will therefore not be out of place to use same methods and techniques in this work. We therefore choose stochastic population models over deterministic models in this project work. This is because the dependence of individual reproduction upon the size of the whole population is best studied in a general branching process context (Jagers and Klebaner, 2011).

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[1] See Chapters Two and Eight of (Grimmet and Stirzaker, 2001) for the definition of random variables and their distributions; and for an introduction to random processes, respectively.

[2] An absorbing state i of a stochastic process is the one in which there is a probability 1 that once the process reaches this state it remains there and never recovers from that state.

1.2 Problem Statement

From the point of view of biology, branching processes are often used to describe stochastic models of the initial stages of population development, while the population is so small that it is not affected by environmental limitations. However, chance events in individual life may decide the fate of the whole population. Thus, the classical Galton-Watson extinction problem emerges as a result of seeking answers to the question of extinction as can be seen (Hamza et al., 2014) and references therein.

Every scientific research is to address a particular problem. Consider a population in a habitat where individuals at the end of each season independently, given the current population size, either split into two new individuals or else just die out. Assume that the probability of an individual splitting into two new ones is influenced by the *carrying capacity* of the habitat, and also by the present size of the population. Assume further that reproduction is sub-critical when the present population size exceeds the carrying capacity of the habitat, and therefore the population has the tendency to decrease in size due to the pressure on available limited resources. Reproduction is supercritical when the present population size is below the carrying capacity of the habitat, and the population has the tendency to increase in size due to abundance of resources. Finally, reproduction is critical when the present population size is equal to the carrying capacity of the habitat, such that it neither increases nor decreases. The project shall investigate the properties of such simulated populations in a number of specific cases.

1.3 Objective of the Study and Research Questions

The main objective of the research is to investigate the dynamics of the binary-splitting population growth model as described in the problem statement section. This will be done through a number of specific cases. The following research questions are addressed in this research.

- Consider a habitat with fixed *carrying capacity* K, and assume that the population evolves in discrete time such that, all individuals live one time unit (or generation or season) and split into two with probability $\frac{K}{K+Z_n}$, if the current population size is Z_n. The development of such simulated populations started from a single individual $Z_0 = 1$, and K of varying sizes, say 100, 1000, and 10000 is studied. Under such circumstances, we wish to address the following extinction-related questions: How often do we observe early extinction before the population attains a steady state? How often do we observe late extinction after the population has once attained a steady state?

  Given the above mentioned values of K, the population will grow up to the vicinity of K, and then linger there for a very long time, but ultimately, it will go extinct [Klebaner et al. (2011); and Haccou et al. (2005)]. But how long before it goes extinct?

- Next, we replace the constant *carrying capacity* with one that is random. For simplicity and as a first model, we consider the case where for each season (or generation), the *carrying capacity* is either H (high, e.g. good weather) or L (low, e.g. bad weather), where $H > L$. The *carrying capacity* in each season is independent and it is randomly chosen to be either H or L with equal probability. This is based on the assumption that some seasons might be favourable than others. The conditions in future seasons are not influenced by previous seasons, hence conditions are independent, and are purely based on chance. Under such circumstances, we wish to study the dynamics of such simulated populations in the same manner as in the first case, except that in this case the *carrying capacities* each season are chosen randomly according to the descriptions given here.

- Given the random *carrying capacity* model in the second case, can one think of a natural version of such scenarios?
- The above three cases describe a discrete time population dynamics in which population size spans season $0, 1, 2, 3, \ldots$, and all individuals have life span 1. What happens if we change the setting to continuous time: let individuals have independently distributed life spans, for simplicity, exponentially distributed[3] with parameter 1 an individual dying at time t getting two children with probability $\frac{K}{K+Z_t}$, where Z_t denotes the population size at time t started at $t = 0$ with $Z_0 = 1$? Cf. (Sagitov and Shaimerdenova, 2013).

1.4 Purpose of the Study

Most of the work done in the literature concerning this area of population dynamics has been on the successful advancement of the theoretical concepts such as in (Klebaner et al., 2011). These theoretical concepts, therefore serve as the foundation on which this project is based. It is therefore the purpose of this study to compare the simulated results with the established theoretical outcomes to see how well the two results agree. This project work is worth pursuing because through these comparisons, we hope to learn and be able to identify other properties that are not envisaged by the theory.

1.5 Organisation of Thesis

This thesis is organised into five chapters. Chapter One gives the introduction to the study, which includes the background and motivation for carrying out this study. It also includes the objectives and the research questions as well as the purpose of the work.

The Second Chapter is devoted to the review of relevant related literature. This comprises a brief review of the history of population dynamics, a quick look at deterministic population models namely exponential growth and logistic growth models. Chapter Two

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[3] A random variable X is said to have exponential distribution with parameter $\lambda(> 0)$ if it has distribution function $F(x) = 1 - e^{-\lambda x},\ \ x \geq 0$ and density $f_X(x) = \{\begin{smallmatrix}\lambda e^{-\lambda x} \texttt{ for } x\geq 0 \\ 0 \texttt{ for } x<0\end{smallmatrix}$.

also discusses the general Galton-Watson branching process as well as population-size-dependent branching processes. Finally Chapter Two will discuss the theoretical framework of the binary splitting model as laid out in [Haccou et al. (2005); and Klebaner et al. (2011)].

Chapter Three gives the model descriptions and the approaches used in simulating the models. The results of the simulations are presented and discussed in Chapter Four and finally, conclusion and recommendation for further or future work are given in Chapter Five.

2. Review of Related Literature

We shall review some relevant and related literature in this chapter. We shall consider a brief history of population dynamics models from the perspective of Malthus' exponential population growth model, and Verhulst's logistic population model. The rest of the chapter shall be devoted to a review of some of the successful concepts in stochastic population growth models models.

2.1 Brief History of Population Dynamics

In 1798, Thomas Malthus published his essay "On the Principle of Population." The essay, which originated from a conversation with a friend on the subject in the Enquirer of one Mr Godwin's essay on "Avarice and Profusion", sought to discuss the general question of the future improvement of society (Malthus, 1798). Malthus, in the first chapter of his essay, postulated that food, and passion between the sexes are necessary to the existence of man. He referred to these two as the fixed laws of our nature, and that the various operations in the universe are governed by fixed laws.

He further went on to say that the power of population is indefinitely greater than that of the earth to produce subsistence for man. This means that the population of man will be sustainable provided there are enough resources to cater for the increase. Based on this premises, Malthus asserted that population increases in a geometrical ratio, when unchecked, and that subsistence for man increases only in arithmetical ratio (Malthus, 1798). Once again, this simply means that in the abundance of resources, human population will grow without bounds.

In the second chapter of his essay, Malthus observed that the human species will continue to grow unchecked, provided there are unlimited resources, and also that people are pure mannered. In this case no part of the society will have any fear of amply providing for a family. Under such circumstances, the power of the human population will be left to increase unchecked. Comparing the populations of the United States of America and that of Europe, Malthus observed that in the United States of America, where the means of subsistence have been more ample, the manner of the people more pure, and fewer checks on early marriages, the population has been found to double itself every twenty-five years. As a consequence, Malthus proposed a rule " that population, when unchecked, goes on doubling itself every twenty-five years or increases in a geometrical ratio" – (Malthus, 1798).

Malthus observed that the doubling effect of the population will put pressure on the available resources as time increases, forcing people to emigrate from their native lands to seek greener pastures in less populated or uncultivated lands. Applying this principle to the entire earth, Malthus observed that the doubling effect of population growth will bring some hardship and a time of distress on the inhabitants of the earth in the early stages of population development. During this season of distress, the discouragements to marriage, and the difficulty of rearing a family are so great that population is at a stand (Malthus, 1798). Some of these anticipated hardships are unavailability of enough food to feed the growing population, and cheap labour due to the few farms available to work in, resulting in unsatisfactory wages and salaries. However, these hardships will also encourage expansion of farms due to available labour, and also establishment of industries to produce enough food to feed the population. There will therefore be continuous production and tillage of the land until there is enough food produced to take care of the population. Eventually calm will be restored and lives will improve. In latter chapters, Malthus made several other observations about population growth dynamics, several of which have stood the test of time. We refer the reader to (Malthus, 1798) for details.

Four decades later in 1838, Pierre-Francois Verhulst having been inspired by Malthus' essay, published a note "On the Law of Population Growth " [Tsoularis (2001); and Bacaer (2011)]. In this article, Verhulst referred to Malthus' discovery of the the principle that the human population tends to increase in a geometrical ratio so as to double after every twenty-five years. Verhulst, however, noticed that the proposition was beyond dispute if abstraction is made of the increasing difficulty to find food. This led him to assert that increase of the population was therefore limited by the size and the food production capability of the country. He therefore introduced the concept of the population getting closer and closer to a steady state.

This means that the geometric population growth dynamics proposed by Malthus was only possible for a very short time. This was precisely stated by Verhulst that "We shall not insist on the hypothesis of geometric progression, given that it can hold only in very special circumstances; for example, when a fertile territory of almost unlimited size happens to be inhabited by people with an advanced civilization, as was the case for the first American colonies"—(Bacaer, 2011).

In the next section, we present the mathematical equations for the above two models introduced by Malthus and Verhulst.

2.2 Deterministic Population Growth Models

Malthus' principle of the human population growing in a geometric progression is modelled by an exponential growth equation. Verhulst called his model the logistic growth model. These models are expressed in differential equations making them deterministic population growth models.

2.2.1 Exponential Growth Model

The exponential growth model of population dynamics is the simplest realistic population growth model given by

$$\frac{dN}{dt} = rN(t), \tag{2.2.1}$$

where the Malthusian parameter $r > 0$ is called the intrinsic growth rate, which represents the per capita growth rate. $N(t)$ is the population at time t. Equation (2.2.1) has the solution

$$N(t) = N_0 e^{rt},$$

where N_0 is the initial population at $t = 0$. Figure 2.1 shows the results for the numerical solution of the exponential population growth model with different values of the parameter, r starting at an initial population, $N_0 = 10$. We observe that the speed of the growth depends on the value of r.

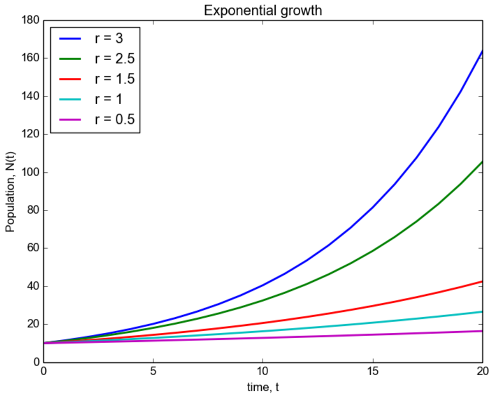

Figure 2.1: Numerical solutions for the exponential growth model for different values of the intrinsic growth rate, r, starting from the same initial population, $N_0 = 10$.

It is however noted that, such exponential growth cannot go on forever. To model the effects of overcrowding and limited resources, population biologists or demographers often assume that the per capita growth rate $\frac{1}{N}\frac{dN}{dt}$ decreases when N becomes sufficiently large, and for small N, the growth rate equals r, just as before (Strogatz, 2015).

2.2.2 Logistic Growth Model

In order to avoid unrestricted growth, Verhulst [Tsoularis (2001); and Bacaer (2011)] observed that a stable population will exhibit a saturation point characteristic of the environment or limited resources. With this observation, Verhulst proposed the following differential equation for the population growth

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{2.2.2}$$

where K is a parameter called the *carrying capacity* of the habitat. When $N(t)$ is small compared to the parameter K, equation (2.2.2) is approximately the exponential growth equation (2.2.1). Verhulst referred to equation (2.2.2) as the logistic equation (Bacaer, 2011). In the literature, the logistic equation is sometimes referred to as Verhulst-Pearl equation, see (Tsoularis, 2001) and references therein, after its originator Verhulst and

Pearl, who used the model to predict the population of the United States of America in 1920. The logistic population growth model has the solution

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)e^{-rt}},$$

where N_0 is the initial population at $t = 0$. An analysis of the above solution to the logistic population growth model reveals the following dynamical features of the population. Firstly, the population increases progressively from $N_0 > 0$ till it reaches its maximum, which is the *carrying capacity* K. The rate of increase is fast initially, but decreases as N gets closer to K.

Secondly, if N is perturbed slightly from the *carrying capacity* K, the perturbation will decay monotonically and $N(t) \to K$ as $t \to \infty$. In other words, the population growth rate becomes negative when the population goes beyond its *carrying capacity*, causing the population to decrease in size until it stabilises to the *carrying capacity* K. The bottom line is that the logistic population growth model has one non-trivial stationary point, which is the *carrying capacity*, i.e. $N^* = K$, and that the population always approaches this point.

Lastly, there is an inflection point, where the population growth rate is maximum, at which the population size is exactly half of the *carrying capacity*. This means that, no matter the initial population size, the growth rate is maximum at the inflection point. The growth rate is therefore increasing, and hence the growth of the population is fast as long as $N(t) < \frac{K}{2}$. On the other hand, when $N(t) > \frac{K}{2}$, the growth rate begins to decrease and hence the the growth of the population slows down. The growth rate $\frac{dN}{dt}$ becomes negative when $N(t) > K$, which causes the population to decrease in size.

All the features discussed above are summarised in figures 2.2, 2.3, and 2.4. Figure 2.2 shows the numerical results of the solution to equation (2.2.2) for different values of the intrinsic growth rate r, for a *carrying capacity* $K = 100$, and initial population size $N_0 = 10$. The figure clearly demonstrates that the population grows progressively from its initial size until it reaches its maximum, which is equal to the value of the *carrying capacity*. This dynamics, however, becomes prominent for larger values of r. The figure also indicates that the growth is fast initially but, it slows down as the population size gets closer to the *carrying capacity*.

In figure 2.3, we observe that for given values of r, and K, any population that starts below K ultimately increases up to K. If the initial population is below the inflection point ($N = 50$ in this case), the increase is fast until it has reached the inflection point, after which it slows down to K. If the initial population is slightly above the inflection point, it increases slowly until it hits K. On the other hand, any population started above K decreases until it comes to K. The picture depicts that once the population has reached its maximum K, it never leaves this point, confirming that $N^* = K$ is a stable fixed point.

Figure 2.4 shows the plots of the growth rate $\frac{dN}{dt}$ against population size N for different values of the intrinsic growth rate r. The various plots show that the growth rate of the population is maximum at the inflection point $\frac{K}{2}$ (50 in this case).

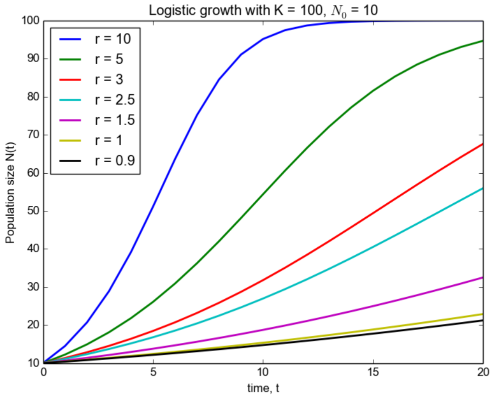

Figure 2.2: Numerical solutions for the logistic model for different values of the intrinsic growth rate, r, starting from the same initial population, $N_0 = 10$

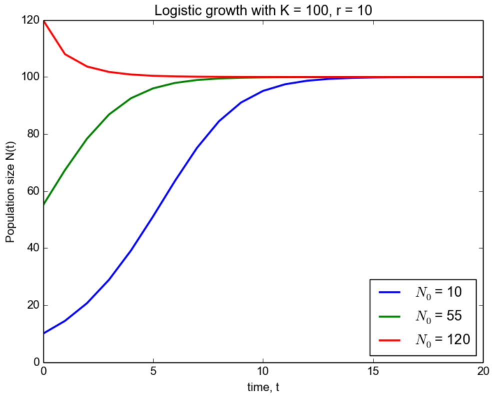

Figure 2.3: Numerical solutions for the logistic model for one value of the intrinsic growth rate, r, starting from different initial populations.

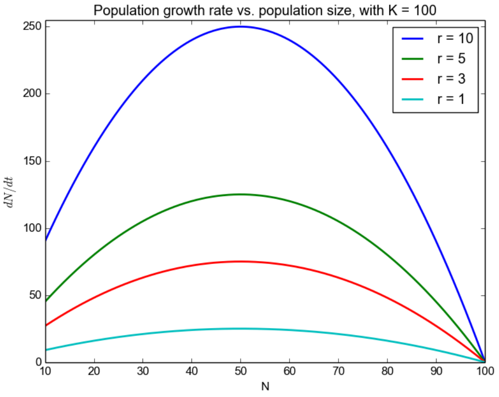

Figure 2.4: Population growth rate against population size.

2.3 Simple Galton-Watson Branching Processes

A so-called merciless dichotomy of population dynamics states that all biological populations either die out or else increase beyond bounds. Based on this assertion, we realise that the deterministic population growth models described above do not give us the whole picture. In order to address the question of extinction, we need stochastic population growth models instead of the deterministic counterparts. In this section we shall give a review of the most successful approach to stochastic population dynamics modelling through the lenses of branching processes. We refer the reader to the introductory chapter of (Jagers, 1975) for a concise historical background of branching processes.

Branching processes refer to individual-based models for the growth of populations. The subject matter of branching processes is usually to give probabilistic descriptions of life careers in order to deduce properties of the processes (i.e., of populations) from the probability laws of individual childbearing and life spans (Haccou et al., 2005). The simplest form of a branching process is the one that stems from a single ancestry, known as the one-type process (Jagers, 1975). The number of children an individual in the population can have is an integer-valued random variable ξ. The ξ's are independent and identically distributed (i.i.d). A Galton-Watson branching process is therefore a stochastic process that counts the number of offspring (or children) of individuals in the population from generation to generation. The distribution of such a process is governed by the probability (or reproduction) law $\{p_k; k \in \mathbb{Z}^+\}$. Thus, the sequence $\{Z_n; n \in \mathbb{Z}^+\}$, where Z_n is the total number of offspring in generation n, explicitly defines a Galton-Watson process.

It is to be emphasised that Galton-Watson processes, $\{Z_n; n \in \mathbb{Z}^+\}$, are discrete-time processes with non-overlapping generations, and only one type of ancestry (Haccou et al., 2005). Each descendant of such a discrete-time process have a life span of one time unit, and at death splits into ξ new descendants [Jagers (1975); Haccou et al. (2005); and Klebaner et al. (2011)]. The process usually starts with an initial population of Z_0 (usually, $Z_0 = 1$) descendants. Each descendant produces a random number of offspring and then dies. The reproduction and survival of descendants are independent in nature. In the next generation, the population size Z_{n+1}, can be determined by summing the numbers of offspring of descendants at death. These individuals then reproduce, giving the next generation, and so on.

Thus, we can denote the number of offspring of descendant j in generation n by ξ_{nj}. Then $\{\xi_{nj}; n \in \mathbb{N}, j \in \mathbb{N}\}$ is a collection of independent and identically distributed random variables, and we can write

$$\begin{aligned} Z_0 &= 1 \\ Z_{n+1} &= \sum_{j=1}^{z_n} \xi_{nj}, \quad n \in \mathbb{N}. \end{aligned} \tag{2.3.1}$$

Under such circumstances, the sequence $\{Z_n\}$ given recursively by the process (2.3.1) is said (Jagers, 1975) to have the same probability distribution as a Galton-Watson process.

If we denote by $\mathcal{F}_n = \sigma(Z_0, z_1, ..., Z_n)$ the σ-algebra (i.e information) generated by the process values $z_0, Z_1, ..., z_n$, then conditional on $\mathcal{F}_n$, we have

$$\mathbb{P}[Z_{n+1} = k|\mathcal{F}_n] = \mathbb{P}\left[\sum_{j=1}^{Z_n} \xi_{nj} = k|Z_n\right].$$

The above shows that the sequence $\{Z_n\}$ is a homogeneous Markov chain with transition probabilities given by

$$p_{lk} = \mathbb{P}[Z_{n+1} = k|Z_n = l] = p_k^{*l}, \tag{2.3.2}$$

where p_k^{*l} is the notation for the l-th convolution power[1] [2] of the offspring distribution $\{p_k; k \in \mathbb{Z}^+\}$. Alternatively, conditional on $Z_n = j$, the distribution of Z_{n+1} is the distribution of the sum of i.i.d. random variables each with distribution $\{p_k; k \in \mathbb{Z}^+\}$. Thus the Galton-Watson process is a discrete-time Markov process and hence possesses the Markov property (Grimmet and Stirzaker, 2001) that future process values (i.e. population) only depends on the present, but not the past history. This is just another way of saying that reproduction in different generations is independent.

Historically, the first population dynamics question tackled with the help of branching processes was that of population extinction: what is the probability that a population dies out (or goes extinct)? Other classic topics are the possible stabilisation of population sizes, growth rates, and age distributions or other aspects of population composition. The solution to the question of extinction probability was first attempted by the clergyman Henry W. Watson in 1873 in response to a challenge posed by Francis Galton in the April 1 edition of the Educational Times – leading to the name Galton-Watson process [Grimmet and Stirzaker (2001); and Jagers (1975)]. The correct solution was, however, provided by J. F. Steffensen in 1930. Prior to that, I. J. Bienayme had earlier realized what the extinction probability should be, and J. B. S. Haldane also later realised what the extinction probability should be, but they both failed to provide the required reasoning [Grimmet and Stirzaker (2001); Haccou et al. (2005); and Jagers (1975)]. The offspring distribution $\{p_k; k \in \mathbb{Z}^+\}$ has mean $\mu > 0$ and variance $\sigma^2 > 0$.

2.3.1 The Mean of a Galton-Watson Process

Using the recursion (2.3.1), we obtain the mean number of offspring of the Galton-Watson process as follows. Each descendant j in generation n has a mean number of offspring $\mu = \mathbb{E}[\xi_{nj}]$. Let

$$M_n = \mathbb{E}[Z_n] = \sum_{k=0}^{\infty} k\mathbb{P}[Z_n = k]$$

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[1] Given two independent random variables X and Y with mass functions f_X, and f_Y respectively, the mass function of the sum of X and Y is denoted by the convolution $f_{X+Y} = f_X * f_Y$, where $*$ is the convolution operator such that $f_X * f_Y(z) = \sum_x f_X(x) f_Y(z - x)$. See Grimmet and Stirzaker (2001) for more.

[2] Convolution power refers to the n-fold iteration of the convolution with itself. By definition, if f is a $d-$dimensional function, and n is a positive integer, then the convolution power is given by $f^{*n} = f * f * f * ... * f * f$, $f^{*0} = \delta_0$, where δ_0 is the $d-$dimensional Dirac delta function. See Feller (1971) for more.

be the mean of the Galton-Watson process in generation n. Then we have that

$$M_{n+1} = \mathbb{E}[Z_{n+1}] = \mathbb{E}\left[\sum_{j=1}^{Z_n} \xi_{nj}\right],$$

$$= \sum_{k=0}^{\infty} \mathbb{P}[Z_n = k]\mathbb{E}\left[\sum_{j=1}^{k} \xi_{nj}\right],$$

$$= \mu \sum_{k=0}^{\infty} k\mathbb{P}[Z_n = k],$$

$$= \mu M_n.$$

From the recursion (2.3.1), we observe that

$$M_0 = \mathbb{E}[Z_0] = 1.$$

We therefore iteratively obtain

$$M_n = \mathbb{E}[Z_n] = \mu^n. \tag{2.3.3}$$

2.3.2 The Variance of a Galton-Watson Process

The variance of the offspring distribution of a Galton-Watson process is determined recursively as follows. Let

$$V_n = Var(Z_n) = \mathbb{E}[Z_n - \mathbb{E}[Z_n]]^2.$$

We recall from probability theory that, given two random variables X, Y, the variance of X can be expressed in terms of conditional expectation and conditional variance as

$$Var(X) = \mathbb{E}[Var(X|Y)] + Var(\mathbb{E}[X|Y]).$$

Applying the above to the current situation, we have that

$$V_{n+1} = Var(Z_{n+1}) = \mathbb{E}[Var(Z_{n+1}|Z_n)] + Var(\mathbb{E}[Z_{n+1}|Z_n]). \tag{2.3.4}$$

Now, since the number of offspring, $\xi_j s$, of descendants in each generation are independent, we have that

$$\mathbb{E}[Z_{n+1}|Z_n] = \mathbb{E}\left[\left(\sum_{j=1}^{Z_n} \xi_j\right)|Z_n\right] = \mathbb{E}[\xi_1 + \xi_2 + ... + \xi_{Z_n}|Z_n] = \mu Z_n, \tag{2.3.5}$$

and

$$Var(Z_{n+1}|Z_n) = Var\left(\sum_{j=1}^{Z_n} \xi_j\right) = Var(\xi_1 + \xi_2 + ... + \xi_{Z_n}) = \sigma^2 Z_n. \tag{2.3.6}$$

Equations (2.3.5) and (2.3.6) together with (2.3.3) now reduce equation (2.3.4) to

$$V_{n+1} = \sigma^2 M_n + \mu^2 V_n.$$

From the recursion (2.3.1), we have that

$$M_0 = 1, \text{ and } V_0 = 0.$$

Thus we have the variance of the process iteratively as

$$V_n = \sigma^2 \mu^{n-1} \sum_{k=1}^{n} \mu^{k-1}.$$

The conclusion is that

$$\begin{aligned} V_n &= n\sigma^2 \quad , \texttt{ if } \mu = 1 \\ V_n &= \frac{\sigma^2 \mu^{n-1} (\mu^n - 1)}{\mu - 1} \quad , \texttt{ if } \mu \neq 1. \end{aligned} \tag{2.3.7}$$

From equations (2.3.3), and (2.3.7) for the mean and variance of a Galton-Watson process, respectively, we observe the following:

- $\mu > 1 \Rightarrow \mathbb{E}[z_n] \to \infty$ as $n \to \infty$. This means that both the population mean and the variance grow exponentially or geometrically in n. In this case, we refer to the process as **supercritical.**
- $\mu = 1 \Rightarrow \mathbb{E}[z_n] = 1 \texttt{ for all } n$. In this case the mean does not change, but the variance increases linearly in n. The process is thus referred to as **critical.**
- $\mu < 1 \Rightarrow \mathbb{E}[z_n] \to 0$ as $n \to \infty$. The mean and the variance both decay exponentially or geometrically. Such a process is known as **subcritical.**

2.3.3 The Generating Function of a Galton-Watson Process

As a stochastic process, every detail of the Galton-Watson branching process can be studied via its probability generating function. The probability generating function of a Galton-Watson branching process, $\{Z_n, n \in \mathbb{Z}^+\}$, is defined (Jagers, 1975) as

$$f_n(s) = \mathbb{E}\left[s^{Z_n}\right] = \sum_{k=0}^{\infty} s^k \mathbb{P}[Z_n = k],$$

for $0 \leq s \leq 1$. The recursion (2.3.1) means that the generating function of the Galton-Watson process is the n-fold composition of itself (Jagers, 1975). Thus, we can write $f_n(s)$ recursively as

$$\begin{aligned} f_0(s) &= s, \\ f_{n+1}(s) &= f(f_n(s)) = f_n(f(s)) \texttt{ for all } n. \end{aligned} \tag{2.3.8}$$

The following properties hold for the generating function of a Galton-Watson process:

- $f(s)$ is a strictly increasing function on the closed unit interval $0 \leq s \leq 1$.
- $f(s)$ is strictly convex, with a strictly increasing first derivative.
- $f(1) = 1$.
- If $\mu \leq 1$, i.e. for both critical and subcritical processes, $f(s) > s$ for $s \in [0, 1)$.
- if $\mu > 1$, i.e. supercritical, the fixed point equation $f(s) = s$ has a unique root in $[0, 1)$.

2.4 The Extinction Probability

The event $\{Z_n \to 0\}$ of a Galton-Watson process is called the extinction of the process (Jagers, 1975). That is to say that for some n, if the process value (or population size) $Z_n = 0$, then the population is said to be extinct. We denote by $t_{ext} = min\{n : Z_n = 0\}$, the **extinction time** if there is such an n and $t_{ext} = \infty$ if there is no such n. In a Galton-Watson process, one is usually interested in the question: what is the probability $\mathbb{P}[t_{ext} < \infty]$ of extinction?

To answer the above question, we proceed as follows. We observe that for some k, $Z_k = 0 \Rightarrow Z_n = 0$ for $n \geq k$. This means that once the processes goes extinct it never recovers from it. Thus, the Galton-Watson process has one absorbing state. Now we can write

$$q = \mathbb{P}[Z_n \to 0]$$

for the extinction probability. Then using the recursive nature of the Galton-Watson process, we have (Jagers, 1975) that

$$\begin{aligned} q &= \mathbb{P}[Z_n = 0 \texttt{ for some } n] \\ &= \lim_{n\to\infty} \mathbb{P}\left[\cup_{k=1}^{n}\{Z_k = 0\}\right] = \lim_{n\to\infty} \mathbb{P}[Z_n = 0] = \lim_{n\to\infty} f_n(0). \end{aligned} \tag{2.4.1}$$

This means that we can always recover the extinction event from the generating function, $f_n(s)$, of the Galton-Watson process:

$$\mathbb{P}[Z_n = 0] = f_n(0).$$

Consequently, by the recursive nature of the Galton-Watson process, these probabilities are non-decreasing in n since we get stuck in the absorbing state, i.e. if $Z_n = 0$, then $Z_{n+1} = 0$. This implies that the limit (2.4.1) exits, and its value is equal to the extinction probability of the Galton-Watson process. The value of the limit, and hence the extinction probability is given by the roots of the fixed-point equation $f(s) = s$, which has two roots $s = 1$, and $s = s^* \neq 1$. The root $s = 1$ is trivial and therefore is not of interest. Discarding the trivial case, we have the following result:

Theorem 2.4.1. *The fixed-point equation* $f(s) = s$ *has exactly one root in* $[0, 1)$ *if* $\mu > 1$ *and none if* $\mu \leq 1$. *The extinction probability* q *is the smallest non-negative root* *of the equation, that is*

$$\mu > 1 \Rightarrow q < 1,$$

$$\mu = 1 \Rightarrow q = 1,$$

$$\mu < 1 \Rightarrow q = 1.$$

Thus, in the critical and subcritical cases, extinction is certain. In the supercritical case, the probability of extinction is given by the unique root $q < 1$ of the fixed-point equation. We refer the reader to (Jagers, 1975) for the proof of the above theorem and also to (Haccou et al., 2005) for further reading.

In the binary-splitting Galton-Watson process, we can use the above theorem to determine the extinction probability as follows. Let the probability of a descendant of the process successfully splitting into two be a, and the complementary probability of dying out be $1 - a$. Then from the probability generating function (2.3.8), we have that

$$f_n(s) = \sum_{k=0}^{\infty} s^k \mathbb{P}[z_n = k],$$

$$f_1(s) = f(s) = s^0 \mathbb{P}[z_1 = 0] + s^2 \mathbb{P}[z_1 = 2],$$

$$\Rightarrow f(s) = 1 - a + as^2.$$

The fixed-point equation is thus given by

$$s = 1 - a + as^2,$$

which has a non-trivial root

$$s^* = \frac{1-a}{a}.$$

Hence the extinction probability of the Galton-Watson binary splitting process is given by

$$q = \frac{1-a}{a}, \ \texttt{for} \ a > \frac{1}{2}.$$

It turns out that the extinction probability of the binary splitting process is the ratio of the probability of a descendant dying out to that of successfully splitting into two.

2.5 Population-Size-Dependent Branching Processes

Population-size-dependent branching processes are Galton-Watson branching processes in which the offspring distribution is a function of the current population size. In other words, reproduction is influenced by the population size. Such processes may exhibit behaviours that may not be encountered in the classical models (Athreya and Jagers, 1997). We denote by $\xi(z)$ the random variable with reproduction distribution $\mathbb{P}[\xi(z) = k] = p_k(z),\ \ k = 0, 1, 2, ...$, and let it represent the number of offspring in a Galton-Watson process with current population size z. Given that the size of the population in generation n is Z_n, and using the fact that the process is Markov (i.e. process values are conditionally independent), the process can be defined recursively [Haccou et al. (2005); and Athreya and Jagers (1997)] as

$$Z_{n+1} = \sum_{j=1}^{Z_n} \xi_{nj}(Z_n), \tag{2.5.1}$$

where z_0 is taken to be a non-negative integer.

Consider a near-critical process in which the offspring mean $\mu(z) \to 1$ as $z \to \infty$. A typical example of such a process is binary splitting. When population size is z, each descendant splits into two with probability $p(z)$ or dies out with probability $1 - p(z)$ independently of all other descendants (Athreya and Jagers, 1997). The process is supercritical with extinction probability less than one [see chapter five of the book by (Haccou et al., 2005) for detailed treatment and the derivation]. However, it does not exhibit the exponential growth associated with supercritical processes (Athreya and Jagers, 1997).

2.6 Bare Bones

In what follows, we shall consider another binary-splitting Galton-Watson type population growth model in which the offspring distribution does not only depend on the population size but also on the environment via its carrying capacity K. In this model, given the current population z, the probability of a descendant successfully splitting into two new ones is given by $\frac{K}{K+z}$, and reproduction is done independently. In such a model, just like any Galton-Watson process, only the successive-non-overlapping generation sizes are counted, that is, every member has the same life-span of one generation (Klebaner et al., 2011).

The process is thus, a population-size-dependent Galton-Watson branching process. It is more formally defined (Klebaner et al., 2011) recursively as:

$$Z_0 = z, \ \ \texttt{a positive integer}$$

$$Z_{n+1} = \sum_{j=1}^{Z_n} \xi_{nj}, \tag{2.6.1}$$

$$\mathbb{P}[\xi_{nj} = 2|Z_n] = \frac{K}{K + Z_n}, \ \ \mathbb{P}[\xi_{nj} = 0|Z_n] = \frac{Z_n}{K + Z_n}.$$

The random variables ξ_{nj} representing the number of offspring j in generation n, are independent and identically distributed given the underlying σ-algebra $\mathcal{F}_n = \sigma(Z_0, Z_1, ..., Z_n)$.

The process therefore is Markovian. The carrying capacity K is taken to be large. The above process thus, behaves like a supercritical process when the population size is far below the carrying capacity, i.e. $Z_n \ll K$. In each generation, this corresponds to a classical Galton-Watson branching process with $\mu > 1$. If it does not die out early, the population tends to increase and it is prone to reach higher values around K before ultimate extinction[3]. It has been shown by (Klebaner et al., 2011) that the time to extinction is very large. The population therefore, if it does not die out early, settles at a quasi-stationary regime, fluctuating around K for a time period that is exponentially long in K, until finally going extinct. For the derivation of the above facts, we refer the reader to (Klebaner et al., 2011).

We rewrite the probability of a descendant splitting into two as

$$a = \frac{1}{1+\frac{r}{K}},$$

where r is the present population size considered to be fixed such that $1 \leq r \leq K$. Then the extinction probability for a classical, not population-size-dependent branching process with this splitting probability a, and a fixed r in the given interval will be given as before, by the nontrivial root of the fixed-point equation

$$q = 1 - a + aq^2,$$

which is

$$q = \frac{1-a}{a} \ \texttt{for} \ a > \frac{1}{2}.$$

The case where $z_n > K$ corresponds to a classical Galton-Watson process with mean number of offspring, $\mu < 1$. The process then behaves like a subcritical process. The population size tends to decrease in n. In the vicinity of K, the process is described as near-critical, and the population size tends to grow linearly in n. The near-critical case is therefore a consequence of the 'merciless dichotomy of population dynamics' (or in the present Markovian case, of the fact that zero is the only absorbing state; see (Grimmet and Stirzaker, 2001)). The population therefore, does not die out early. It lingers around the critical value for a very long time before it ultimately goes extinct with extinction probability

$$\mathbb{P}[z_n \to 0, \ \texttt{as} \ n \to \infty] = 1.$$

This is shown in [Haccou et al. (2005); and Klebaner (1984)]. We wish to state a very powerful and useful proposition from (Klebaner et al., 2011) below:

Proposition 2.6.1. Whatever the starting number z, carrying capacity K, and time (generation) n,

$$\mathbb{P}_z(T > n) \leq \left(1 - e^{-K}\right)^n \leq \exp\{-ne^{-K}\}$$

and

$$\mathbb{E}_z[T] \leq e^K,$$

where T is the time to extinction.

---

[3] Ultimate extinction is when no individuals exist after some finite number of generations. The probability of ultimate extinction is always one

We refer the reader to (Klebaner et al., 2011) for the proof of the above proposition. The second part of the above proposition seems to define an upper bound for the expected time to extinction for a supercritical binary splitting process regardless of the starting number.

3. The Model: Description, Analyses, and Simulation

The model considered in this work is a generalised version of a similar model in (Klebaner et al., 2011) (see also equation 2.6.1) for asexual binary-splitting populations. This chapter is therefore devoted to the description, analyses, and the method of simulation of this generalised model for such populations.

3.1 Model Description and Analyses

The model considered in this project is the famous binary-splitting population-size-dependent Galton-Watson process (as found in the literature) with just a slight modification. The model is based on the following assumptions:

- Simple population – the population considered is that of a single trait or one-type or single-type.
- All individuals have a life-span of one season or generation.
- At death, individuals either split into two new ones or just disappear. The splitting or otherwise of individuals is independent, given the current population size.
- The probability of splitting into two new individuals depends on both the current population size and the carrying capacity of the habitat.

The model is therefore a population-size-dependent Galton-Watson branching process that counts the children (or offspring) of individuals of the population in non-overlapping generations. Given the independence nature of reproduction, the number of children of an individual in each season is a random variable that takes values zero or two. We denote by $\xi_{n,i}$ the number of children of the $i-th$ individual in the $n-th$ season. We start the process with just a single ancestry and define the evolution of the process recursively (or generally) as

$$Z_0 = 1,$$

$$Z_{n+1} = \sum_{i=1}^{Z_n} \xi_{n,i}, \tag{3.1.1}$$

$$\mathbb{P}[\xi_{n,i} = 2|Z_n] = \frac{vK}{K + Z_n}, \quad \mathbb{P}[\xi_{n,i} = 0|Z_n] = \frac{(1-v)K + Z_n}{K + Z_n}.$$

The random variables $\xi_{n,i}$ are independent and identically distributed, given the current population size Z_n, and or the whole past history of the process, $Z_0, Z_1, Z_2, ..., Z_n$. The parameter K is the carrying capacity of the habitat, which is considered to be large, and

Z_n is the population size in season n. The parameter $v \in (0.5, 1)$ shall sometimes be referred to as the "scaling parameter", and $v = 1$ corresponds to the original model in (2.6.1).

A classical Galton-Watson branching process is called critical when the mean number of offspring is one. Thus, in order to determine the criticality criterion for our model, we will require that

$$\frac{2vK}{K + Z_{critical}} = 1 \Rightarrow Z_{critical} = (2v - 1)K, \tag{3.1.2}$$

where $Z_{critical}$ is the critical population size in any given season.

The original model in (2.6.1) does not really capture the notion of early extinction. This is because given K large, and starting with $Z_0 = 1$, the probability of this single individual splitting into two new ones is

$$\frac{K}{K+1} \approx 1 \texttt{ for } K \texttt{ large },$$

which means that the initial individual always splits into two in the first generation. However, there is a possibility of the initial individual dying out just in the first generation. Hence the introduction of v to 'scale' down the chances of the first individual always splitting in the first generation. The scaling parameter also affects the splitting probability of individuals in subsequent seasons (or generations). The introduction of v also means that the critical population size will no longer be equal to K as shown in equation (3.1.2). The possible values that v can take were chosen based on the form of the this new critical population size.

Thus, the population generated by our model, with a fixed splitting probability, is said to be in a critical stage, where the size of the population neither increases nor decreases, when the population size in season n, $Z_n = Z_{critical}$. It is said to be in a supercritical stage when $Z_n < Z_{critical}$ and the population therefore has the tendency to increase in size. Finally, it is said to be in a subcritical stage when $Z_n > Z_{critical}$ and has the propensity to decrease in size due to limited resources. It is known that for a critical, and a subcritical Galton-Watson branching process extinction is certain, and the extinction probability is, $\mathbb{P}[Z_n \to 0, \texttt{ as } n \to \infty] = 1$ [Haccou et al. (2005); Jagers (1975); and Klebaner et al. (2011)].

For a model of this nature, it has been shown (Klebaner et al., 2011) that when the process starts with Z_0 large, the time to extinction is very large, with an overwhelming probability. The population will therefore settle in a pseudo-stationary state, where the population size fluctuates around the value $(2v - 1)K$ for a time period that is said (Klebaner et al., 2011) to be exponentially long in K, after which it ultimately dies out. Let

$$T = T_{ext} = min\{n : Z_n = 0\}$$

denote the time to extinction of the process. Let the probability of splitting into two for any given size of the population z, and carrying capacity K large be given by

$$a = \frac{vK}{K+z} = \frac{v}{1+b},$$

where $b = \frac{z}{K}$. Similarly, the probability of dying out given a fixed population size z, and carrying capacity K, will be denoted by

$$1 - a = \frac{1 + b - v}{1 + b}.$$

We know [see Klebaner et al. (2011) for the proof] that for any $1 \leq z \leq dK$, and for the special case where $v = 1$,

$$\mathbb{P}_z[T < T_{dK}] < d^z \texttt{ for } 0 < d < 1,$$

where z is the starting value of the process, which is known, fixed, and chosen to be large (i.e. > 1). $\mathbb{P}_z$ is the conditional probability given the current population size, z. Thus, the probability that the process becomes extinct by season n, before reaching the value dK is $\mathbb{P}[Z_n \to 0] = q$, which is smaller than the corresponding probability of ultimate extinction for the classical Galton-Watson process (Klebaner et al., 2011).

From (Jagers, 1975), we know that the probability of extinction is the non-trivial root, $s^* = q$, of the fixed-point equation $f(s) = s$, and from [Haccou et al. (2005); and Klebaner et al. (2011)], it is well known that q is the smallest root of the quadratic equation

$$1 - a + as^2 = s.$$

In this case, such non-trivial root is given by

$$q = \frac{1-a}{a} = \frac{1 - v + \frac{z}{K}}{v}, \texttt{ for } z \texttt{ known and fixed.}$$

Thus, we can write the extinction probability of the process started at a fixed population size $z = 1$ as

$$Q = \frac{1 - v + \frac{1}{K}}{v}.$$

Then we can say that the probability of early extinction is approximately of the order $\frac{1-v+\frac{1}{K}}{v} \sim \frac{1-v}{v}$ for K large.

It has been observed that for a population-size-dependent Galton-Watson process of this kind, the expected time until extinction is exponentially long in K (Klebaner et al., 2011) and proposition 2.6.1 defines a bound for the expected time to extinction for the case where $v = 1$. In what follows, we wish to give a general version of the statement in proposition 2.6.1.

Proposition 3.1.1. Whatever the starting number z, carrying capacity K, the "scaling parameter" v, and time (generation) n,

$$\mathbb{P}_{z,v}(T > n) \leq \left(1 - e^{-vK}\right)^n \leq \exp\{-ne^{-vK}\}$$

and

$$\mathbb{E}_{z,v}[T] \leq e^{vK},$$

where all symbols have their usual meanings.

Proof. We give a proof of the above assertion by using and modifying the arguments used to prove a similar proposition (2.6.1) in (Klebaner et al., 2011).

Define the probability that the population dies out after n generations as

$$Q_n := \mathbb{P}_{z,v}(T > n).$$

Let the present population in generation n be k, where k is a positive integer, that is $Z_n = k, k \in \mathbb{Z}^+$. Given $Z_n = k$, individuals split with probability

$$\frac{vK}{K+k}.$$

Conditional on $Z_n = k$, the probability of not splitting into two children and hence having no offspring is

$$1 - \frac{vK}{K+k}.$$

By independence, the probability that nobody in the $n-th$ generation gets a child, given $Z_n = k$ is

$$\left(1 - \frac{vK}{K+k}\right)^k \geq \left(1 - \frac{vK}{vK+k}\right)^k = \left(\frac{k}{vK+k}\right)^k,$$

and

$$\left(\frac{k}{vK+k}\right)^k = \left(\frac{1}{1+vKk^{-1}}\right)^k \geq e^{-vK},$$

which yields

$$\mathbb{P}_{z,v}(T \leq n+1) = \mathbb{P}_{z,v}(T \leq n) + \sum_{k=1}^{\infty} \mathbb{P}_{z,v}(Z_n = k) \left(\frac{k}{vK+k}\right)^k$$

$$\geq \mathbb{P}_{z,v}(T \leq n) + e^{-vK} Q_n.$$

But,

$$\begin{aligned}
\mathbb{P}_{z,v}(T > n+1) &= 1 - \mathbb{P}_{z,v}(T \leq n+1) \\
&\leq 1 - \left[\mathbb{P}_{z,v}(T \leq n) + e^{-vK} Q_n\right] \\
&= 1 - \left[1 - \mathbb{P}_{z,v}(T > n) + e^{-vK} Q_n\right] \\
&= \mathbb{P}_{z,v}(T > n) - e^{-vK} Q_n.
\end{aligned}$$

Hence,

$$Q_{n+1} \leq \left(1 - e^{-vK}\right) Q_n,$$

and the upper bounds on the probabilities follow by induction and the elementary inequality $0 < 1 - u < e^{-u}$ for $0 < u < 1$. The second assertion follows by summing over all generations as

$$\mathbb{E}_{z,v}[T] = \sum_n \mathbb{P}_{z,v}(T > n) \leq \sum_n \left(1 - e^{-vK}\right)^n = e^{vK}.$$

□

An estimate for a corresponding lower bound can be deduced in a similar manner, but since this is very small compared to the upper bound, as we will show with our simulated results, we do not derive it. As we have already learnt, with a non-zero probability, the population will grow from any given starting point till it comes to the vicinity of the critical value $Z_{critical} = (2v-1)K$. In this near-critical stage, the probability of an individual splitting into two is

$$\frac{vK}{K + Z_{critical}} \approx \frac{1}{2}$$

regardless of the value of v. We there anticipate that the population size will stay and fluctuate around the critical value for a very long time before it embarks on the path to extinction. This means that the currently derived upper exponential bound indeed gives a survival time of the right order. Similar arguments can be found in (Klebaner et al., 2011).

3.2 Model Simulation

In this section we outline the different cases considered for this work and how the simulations were carried out. The above model is simulated using the Python programming language [see Python Software Foundation. Python Language Reference, Available at http://www.python.org].

3.2.1 Fixed Carrying Capacities

In the case of fixed carrying capacities, we assign fixed numbers to the carrying capacity, K, for all seasons, such as $K = 100, 1000, 10000$. We first of all consider a discrete season scenario, where seasons are discrete. The number of offspring of individual i in season n, $\xi_{n,i}$ are independent and identically distributed twice Bernoulli random variables (Klebaner et al., 2011). Thus, for each value of K, starting from a single ancestor, $Z_0 = 1$, we simulate the population in the next season Z_{n+1} given the current population Z_n as twice a binomial random variable with parameters, $(Z_n, p(Z_n))$, that is,

$$Z_{n+1} \sim 2\texttt{Bin}(Z_n, p(Z_n)),$$

where

$$p(Z_n) = \frac{vK}{Z_n + K}$$

for different values of v such as $v = 0.55, 0.6, 0.65, 0.7, 0.8$. This ensures that, given the populations Z_n in season n, the number of individuals in the next season has the distribution of twice binomial random variable, with parameters as given above. Given the inherent nature of binary splitting of individuals in each season, it makes sense to consider the number of individuals in each season as independent binomial distributed random variables.

The advantage of this approach is that, the independent splitting of individuals in each season given their nature, is already captured in the random variable $\texttt{Bin}(Z_n, p(Z_n))$

making it redundant to check the survival or otherwise of each individual in the preceding population. This therefore speeds up our simulation.

For any given set of the parameters (K, v), the model is simulated several times using the given parameter values repeatedly. Quantities such as the probability of early extinction, the probability of late extinction, and the average time to extinction are computed as averages over the number of repetitions or runs performed.

3.2.2 Random Carrying Capacities

Here, we replace the constant (or fixed) carrying capacities in section 3.2.1 with the ones which vary randomly every season. Considering a very simple case, we let the carrying capacity each season be a high or low value chosen randomly. For example low ($K = 100$ for a bad season) or high ($K = 1000$ for a good season) chosen randomly with some predetermined or known probability p. An interesting case being when $p = 0.5$. Since conditions in different seasons are independent and highly unpredictable, we assign equal probabilities to these two types of seasons (namely good or bad).

3.2.3 Continuous Time

If time permits, we shall simulate the continuous time version of our model by considering a population in which individuals live for a time period that is exponentially distributed, and given the current population size, an individual either splits into two or just dies out. The probability of splitting into two or otherwise is the same as given in the the discrete season case. Here, seasons (or time) are no more discrete, but continuous drawn from a distribution, and we replace Z_n with Z_t. The simulation for this case will be carried out in two different ways. In the first approach, we shall assume that the lengths of the seasons are exponentially distributed with parameter $\lambda = 1$. That is, given the initial population size $Z_0 = 1$ at $t = 0$, we randomly select the length of time in the next season, Δt, from an exponential distribution with parameter $\lambda = 1$. That is, if the current population size is Z_t, and we assume that all individuals have the same life span given by the length of the season

$$\Delta t \sim \texttt{Exponential}(\lambda)$$

and that all individuals split together, we have that

$$Z_{t+\Delta t} \sim 2\texttt{Bin}(Z_t, p_{Z_t}),$$

where $p_{Z_t} = \frac{vK}{K+Z_t}$ is the conditional probability of successfully splitting into two given the current population Z_t. The parameters K and v have the usual meaning as in the discrete time model above.

The second approach, will be to look at the whole process as a birth-death process in which the population will evolve from season to season according to a birth rate λ and a death rate μ. We will further assume that each individual in the population has an exponentially distributed life span. The splitting or otherwise of individuals will happen at different times, which means some individuals in the population may live longer than others.

3.3 Technical Resources

Majority of the simulations for this work were done on personal laptop. The operating system on this laptop is a Linux distribution Ubuntu 14.04. Some of the simulations especially, those that took very long time to run were carried out on one of the Linux computers in one of the computer labs in the physics building at Chalmers.

4. Results

We discuss the results of our simulations in this chapter. The discussion is grouped under appropriate headings as shown in the preceding sections. The results of our simulations are mainly shown in graphs for easy understanding and articulation. This also makes it easy for one to follow the discussion and the arguments put forward thereof.

4.1 Probability of Early Extinction for Discrete Seasons

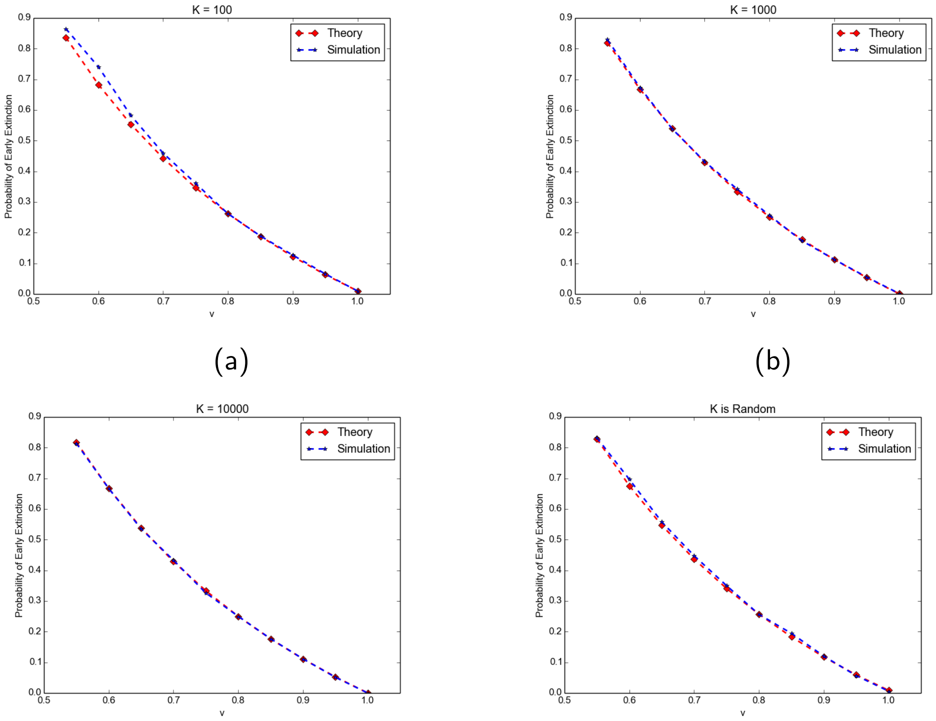
For the purposes of computing the empirical probability (or proportion) of extinction, we classified extinction as either early or late based on a threshold number. For simplicity, the threshold number was chosen to be the critical population size, which depends on the parameters K and v, and is given by $Z_{critical} = (2v-1)K$, where K is fixed. For a random K, which is chosen with equal probability to be L or H, the threshold value was chosen to be $Z_{threshold} = (2v-1)L$. If the population goes extinct, i.e. $\{Z_n = 0 \texttt{ for some } n \geq 1\}$, before ever reaching the threshold number, the extinction is categorised as early extinction. Otherwise, it is deemed late extinction. For a fixed value of the carrying capacity K, the simulation was run over values of $v = 0.55, 0.6, 0.65, 0.7, 0.75, 0.8, 0.85, 0.9, 0.95, 1.0$. For each pair (K, v), the simulation was repeated 10000 times and the frequencies of early extinctions were recorded. The empirical probability of early extinction was computed as a proportion

$$\frac{\texttt{frequency of early extinction}}{10000}.$$

In the case of random K, the above result was further averaged over another 10000 Monte Carlo steps before comparing with the theoretical values. The probabilities of late extinctions were not computed since they can be deduced directly from that of early extinctions for each pair (K, v). The results of the simulation are compared with the theory, and are shown in figure 4.1 (a) - (d).

Figures 4.1 (a) - (c) show the results for fixed values of K, and figure 4.1d shows the results for random K. Apart from the case $K = 100$, i.e. figure 4.1a, there was perfect agreement between the simulated results and the theoretical results for all values of v. The differences in the theoretical and the simulated results in figure 4.1a for values of $v < 0.75$ is as a result of the associated fluctuations in the population size for such lower values of v. This means that if $K = 100$, and v is small, there are higher fluctuations, which increase the chances of observing early extinctions. These fluctuations, however, begin to stabilise as v becomes large and the population settles to a pseudo-stationary phase at which state early extinction becomes rare just as in the first model by (Klebaner et al., 2011). The effects of the fluctuations on the chances of observing early extinctions are discussed further subsequently in this chapter. As a consequence, for all values of K, when v is small, early extinctions happen quite often. However, as v approaches one, the probability of early extinction is very small, almost zero but not negligible, as shown in figure 4.1. Conversely, the probability of late extinction approaches one as K approaches infinity and v approaches one. The result is also true for finite but random K. Thus, we can assert that extinction is certain for a binary splitting process started with a single ancestry, and this is supported by both the theoretical arguments presented in [Haccou et al. (2005); Klebaner et al. (2011); and Klebaner (1984)] and the simulations.

Looking at the results for the probability of late extinction as discussed above, it is tempting to conclude that since the probability of late extinction is approximately one, we are likely to observe these extinctions quite often for any given set of the parameter values. However, as shown in the next section, extinction does not show up as often as we expect, especially for larger values of K that we consider in this work. Figures 4.1b and 4.1c suggest that results for fixed larger values of the carrying capacity K are not that interesting as compared to results from the case where we allow the carrying capacity to be random shown in figure 4.1d.



(a) (b)

(c) (d)

Figure 4.1: Probability of early extinction

4.2 Evolution of Population, and Extinction Time for Discrete Seasons

In this section, we show some results for the evolution of our process over the discrete seasons. Figure 4.2 shows results for $K = 100$ for selected values of v. Results for $K = 1000$, and K random are shown in figures 4.3, and 4.4 respectively. Results for values of $K > 1000$ were not shown since such results exhibit the same characteristics as those shown for $K = 1000$. For each pair (K, v) of the parameters, we repeated the simulation five times (or trials) and the five results were plotted. The different scenarios are shown in the sub-figures.

The results for $K = 100$ shown in figure 4.2 seem to suggest that we are likely to observe both early and late extinction most of the time. For instance, in sub-figures 4.2a - 4.2e both types of extinction were observed. These sub-figures show that the number of late extinctions tend to increase and that of early extinctions tend to decrease as we increase the parameter v from 0.55 to 0.75 in steps of 0.05. Also, the time to ultimate extinction increases tremendously as v increases. For $v = 0.55$, the expected time to extinction seems to be of the order ~ 10. The expected time to extinction for values $v = 0.6, 0.65, 0.7,$ and 0.75 are of the order $\sim 10^2$, $\sim 10^3$, $\sim 10^4 - 10^6$, and $\sim 10^8$ respectively as shown in the table below.

K = 100

v	$\mathbb{E}_{1,v}[T]$	e^{100v}
0.55	11.42 ~ 10	7.69×10^{23}
0.60	57.38 $\sim 10^2$	1.14×10^{26}
0.65	1934.11 $\sim 10^3$	1.69×10^{28}
0.70	405456 $\sim 10^5$	2.52×10^{30}
0.75	160875042 $\sim 10^8$	3.73×10^{32}

Table 4.1: Simulated results for expected time to extinction for a fixed K compared with upper bound.

The second column of table 4.1 corresponds to the simulated results for the extinction times averaged over 100 repetitions of our model for fixed $K = 100$, and selected values of v. The third column shows values of the upper bound for each pair of the parameter values (K, v).

The above observations suggest that the expected time to extinction increases as v increases for a fixed K. A first look at these results suggests that the time to extinction is likely to be exponential in v and K. We cannot tell much at this point since we only know the results for $K = 100$ for now. However, when we compare with the upper bound e^{100v}, we see that the upper bound is extremely large as shown in the third column of the above table. This means that as $v \to 1$, the expected time to extinction will also be extremely large and therefore we would have to wait for a very long time to record such extinction events. This is manifest in the result shown in figure 4.2f. In this figure, we see that after 10^9 generations, the populations for four out of the five trials have not yet gone extinct. The results for $K = 1000$ are not that encouraging as our objective of observing late extinctions and therefore recording the expected time to extinction were not achieved for values of $v > 0.55$. As shown in figure 4.3, we only observe extinction for $v = 0.55$ and most of the time they were early extinctions as depicted in figures 4.3a, and 4.3b. For $v = 0.55$, the time to ultimate extinction averaged over 10 trials was approximately $42014.2 \sim 10^4$ with an upper bound of 7.28×10^{238}. We were not able to record any late extinction times for values of $v > 0.55$. In one instance, when $v = 0.6$, the simulation was left to run for as long as 120 hours (i.e. five days) corresponding to approximately 10^{14} generations for a single trial and the process was still nowhere near extinction. This is however, not that surprising since the upper bound in this case is $e^{600} \sim 10^{260}$. Thus, we would have to wait for a very long time in order to record extinction time. This then is a challenge and therefore limits how far we can go with regards to computing expected time to extinction. Figures 4.3c, 4.3d, 4.3e, and 4.3f show the results for the last 10^8 generations of 10^9 generations for a fixed $K = 1000$ and values of $v = 0.6, 0.8, 0.9$ and 1.0 respectively.

We observe at this point that for fixed values of $K = 100$, and $K = 1000$, if we compare the expected time to extinction for $v = 0.55$, which are $11.4 \sim 10$, and $115.33 \sim 10^4$ respectively, they seem to suggest that the expected time to extinction is indeed exponential in K. However, a plot of the log of the order against selected v values for $K = 100$ shown in figure 4.5 is not a straight line, which also indicates that the expected time to extinction cannot be exponential in v.

On the other hand, results for the evolution of the population for the case where the carrying capacity is random shown in figure 4.4 are a bit interesting when compared to the case where the carrying capacities were fixed and large. We were not able to observe late extinction for $K = 1000$, and $v = 0.6$ as shown in figure 4.3c. However when K was random, we were able to observe late extinction for $v = 0.6$, which is shown in figure 4.4b. Similar observations were made when v was increased to 0.65 and 0.7 as reported in figures 4.4c and 4.4d respectively and also shown in the table 4.2 below.

Random K

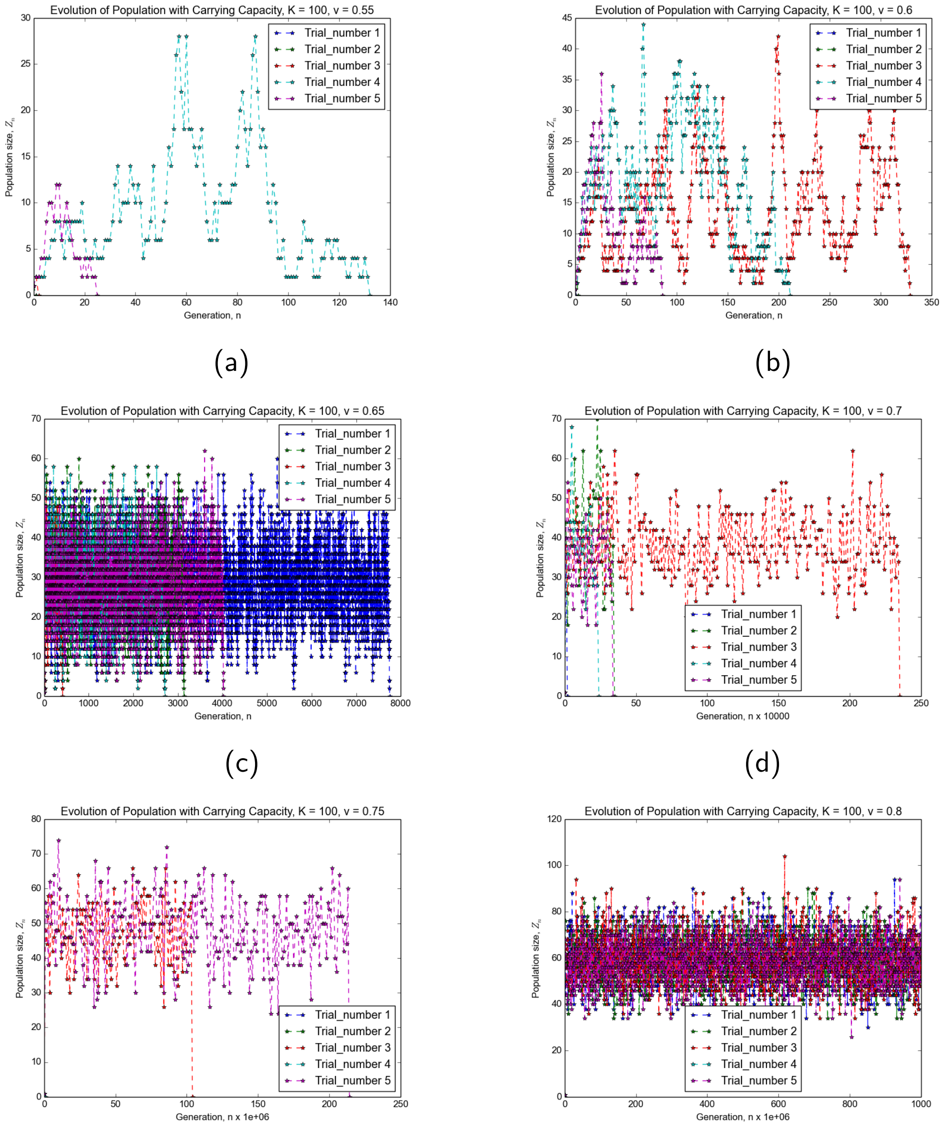
v	$\mathbb{E}_{1,v}[T]$
0.55	115.33 $\sim 10^2$
0.60	1516.67 $\sim 10^3$
0.65	86034.42 $\sim 10^5$
0.70	325024341.6 $\sim 10^8$

Table 4.2: Simulated results for expected time to extinction for randomly varying K.

The order of expected time to extinction for the case where K is random for some selected values of $v = 0.55, 0.6, 0.65, 0.7$ are respectively $\sim 10^2$, $\sim 10^3$, $\sim 10^5$, and $\sim 10^8$. These orders of magnitudes suggest once again that the expected time to extinction are still very large even for random K as v approaches unity and for that matter the expected time to extinction is also likely to exponential in K and v. But, figure 4.5 shows that it cannot be exponential in v. However, as of now there is no known upper bound for this case, and we could not therefore compare with such a bound. This also means that we cannot be sure that it is exponential in K since K is random in this case. That not withstanding, we observed that the noise (or fluctuations) in the process for this case increases as v increases since the K is chosen to be either low (i.e $L = 100$) or high (i.e. $H = 1000$) with equal probability in each generation. This then means that we are likely to observe ultimate extinction even for higher values of v closer to 1.

When a plot of the order of the expected time to extinction on a logarithmic scale for random K was compared with a fixed $K = 100$ for selected values of v, we observed that, given the same value of v, the order was large for K random than for $K = 100$.

These results are shown in figure 4.5. The graphs for both cases are not straight lines, which goes to establish that the order is not exponential in v as we have already observed.

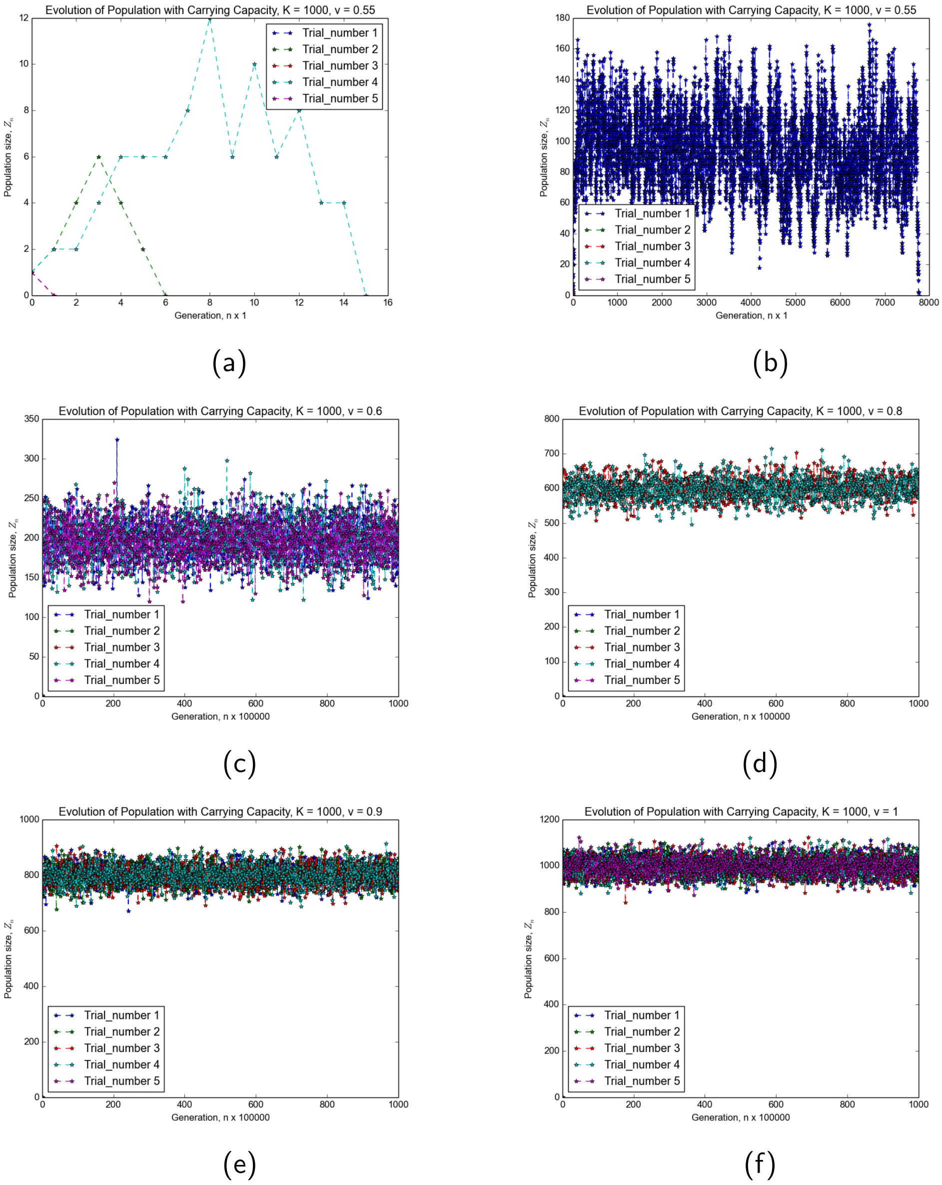


(a) (b)

(c) (d)

(e) (f)

Figure 4.2: Evolution of the process for $K = 100$ and selected values of v

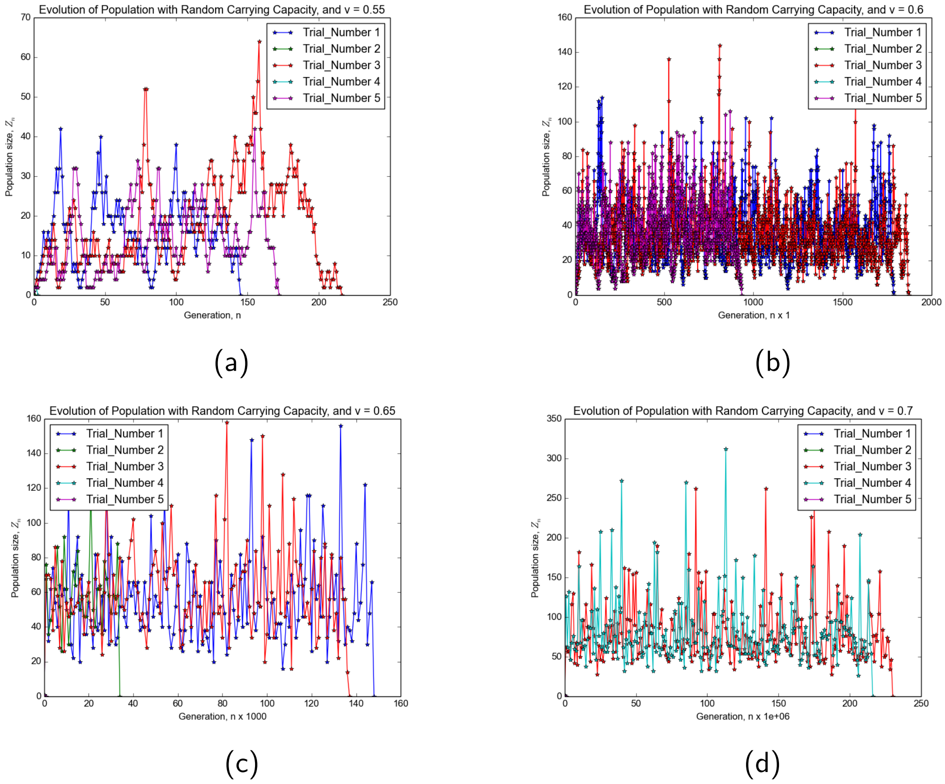


(a) (b)

(c) (d)

(e) (f)

Figure 4.3: Evolution of the process for $K = 1000$ and selected values of v



(a) (b)

(c) (d)

Figure 4.4: Evolution of the process for K random and selected values of v

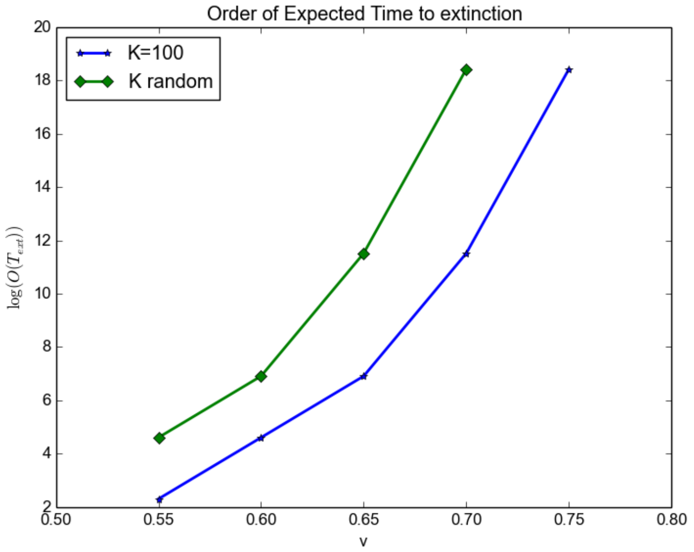


Figure 4.5: Order of expected time to extinction for $K = 100$, and K random

4.3 Pseudo-Stationary-State Distribution, and Risk of Extinction

From our discussion so far, we have come to terms with the fact that it is not possible to observe, and record the expected time to extinction for large fixed K values and values of v approaching one. In view of this we decided to have a look at the effect of the fluctuations in the population when the process had reached the critical stage. As observed in the previous section, the band (or fluctuations) around the critical population size decreases as K approaches infinity, and as v increases. As a result the empirical probabilities of early extinctions were marginally small, almost insignificant, but not negligible. The complementary probabilities of late extinction were however close to one, but take extremely longer time to occur.

We have therefore decided to explore the effects of such fluctuations around the critical value, that is when the process is in the pseudo-stationary state, on the risk of late or ultimate extinction. Such a measure as the risk of extinction does not exist in the literature of the population-size dependent binary splitting processes. However, through a central limit argument, one can show that for the special model where $v = 1$ (Klebaner et al., 2011), the noise or fluctuations in the population, when the process had reached the pseudo-stationary stage, is of order $\sim \frac{1}{\sqrt{K}}$ as $K \to \infty$. This means that as $K \to \infty$, our stochastic model will become less noisy, in which case it will take a very long time before it leaves the band around the critical value. It is therefore not surprising that we were not able to observe extinction for large fixed values of K as $v \to 1$ in the general model.

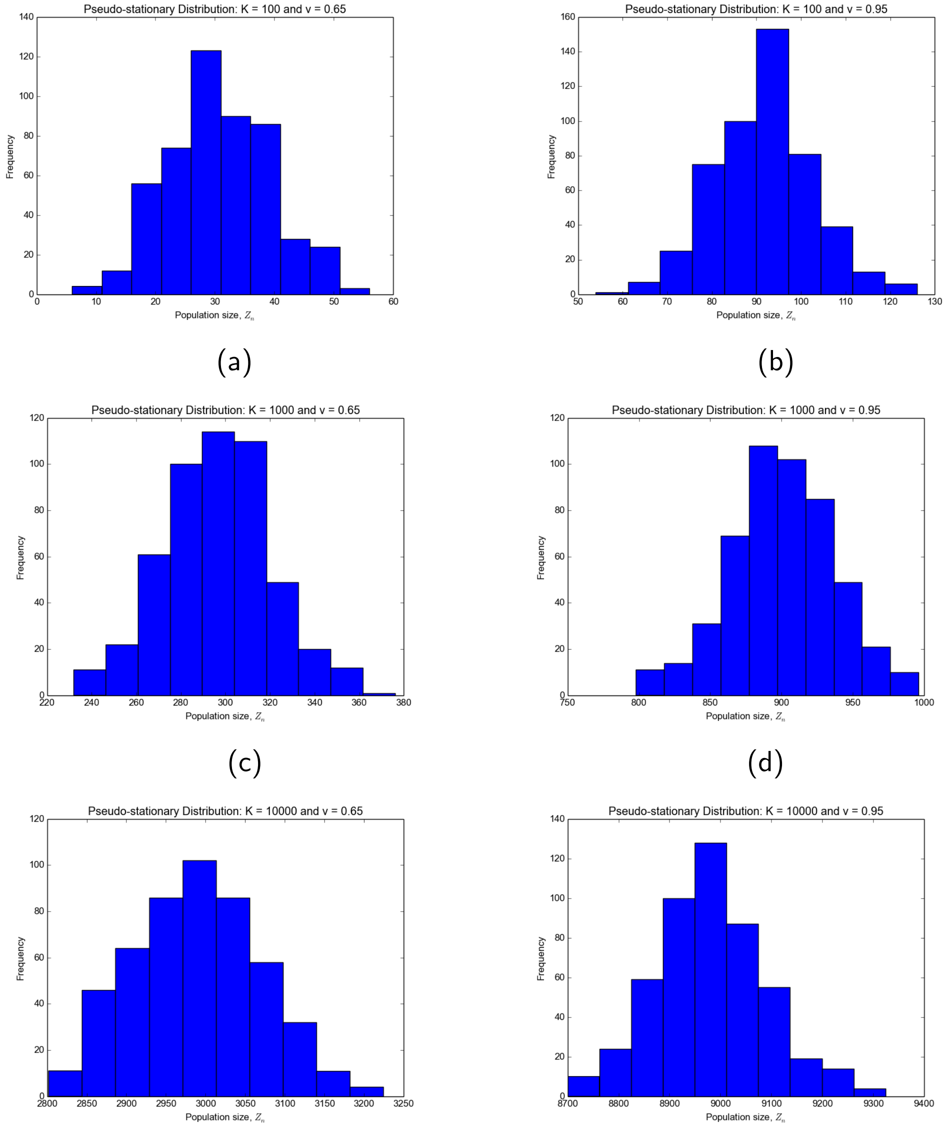
Figure 4.6 shows the empirical pseudo-stationary distribution for the process Z_n using $K = 100$, $K = 1000$, $K = 10000$ as well as random K for $v = 0.65, 0.95$ in each case. The distribution for each pair of parameter values as shown in the figures are approximately Gaussian for the fixed K's, and approximately exponential for the random K's. Using a central limit theorem argument for the fixed K's, we define a corresponding process

$$Y_n = \frac{Z_n}{(2v-1)K}.$$

Then Y_n is approximately Gaussian with mean 1, and standard deviation $\frac{1}{\sqrt{(2v-1)K}}$. Thus, the noise or fluctuations in this corresponding process is of order $\mathcal{O}\left(\frac{1}{\sqrt{(2v-1)K}}\right)$. We can therefore discuss the risk of extinction in terms of the standard deviation of this new process. We observe that

$$\frac{1}{\sqrt{(2v-1)K}} \to 0 \text{ as } K \to \infty.$$

Thus for K large, there is very low risk of the process going extinct as we have already seen in our earlier discussions. For K random however, it is not clear how we can draw similar conclusions using the central limit theorem argument.



(a) (b)

(c) (d)

(e) (f)

Figure 4.6: Empirical Distributions Pseudo-Stationary-States

4.4 Application to Bacterial Growth

In this section, we discuss a possible naturally occurring situations or populations in which our simple model can be applied and also suggest possible modifications to the model.

Bacteria are unicellular microbes whose reproduction is through a process known as binary fission. That is a single bacterium cell divides into two new daughter cells in a fixed amount of time known as the doubling or generation time (Todar, Accessed: May 2016). Different kinds of bacteria have different generation time, for example Escherichia coli has a generation time of 17 minutes and Staphylococcus aureus has $27-30$ minute under favourable conditions (Todar, Accessed: May 2016). Bacterial populations evolve in phases, and there are four phases of bacterial growth. These are:

1. The lag phase: when a bacterium cell is introduced into a new environment, it takes some time for it to adapt to the new environment. During this period, the growth is slow (Prats et al., 2006).
2. The logarithmic or exponential phase: After the adaptation to the new environment, the growth becomes rapid, and this phase is called the exponential or log phase.
3. The stationary phase: The stationary phase is a transition from rapid growth to a stress response state (Hecker and Volker, 2001). The exponential growth is not forever due to factors such as exhaustion of available nutrients, accumulation of inhibitory metabolites or end products, and exhaustion of space (Todar, Accessed: May 2016).
4. Death or 'extinction or ultimate' phase: This is essentially the reverse of the log phase. In the death phase the population begins to decline exponentially.

Results shown in figures 4.2, 4.3, and 4.4 shows that our model exhibits to some extent, with the exception of the lag phase, the dynamics of bacterial population growth. In particular, if we consider the case where we have a varying carrying capacity, we can argue that the randomly varying carrying capacity can represent factors in the host environment. So the carrying capacity in this case will involve factors such as temperature, pH, nutrients, and a bunch of other chemicals that might influence the survival or otherwise of the bacterial cells population. These factors may in themselves be randomly varying in time. A possible modification to cater for these variables will be the one in which the carrying capacity will be a function of such randomly varying factors and also will depend on time. Making it a more complicated situation than what our current model can handle.

For such a population, we might be interested especially, in the time to extinction, that is how long it will take for the bacterial population to die out without any introduction of foreign elements such as antibiotics. This could be beneficial in the administration of medication in the case of pathogenic bacteria. If we can predict the extinction time for a pathogenic bacterial population, we can use such information to track or trace an infection to its stationary phase, where symptoms begin to show and where the population of the pathogens fluctuates around a critical value, which will give us an idea of the average size of the population in that phase, so that effective prescription of medication can be made.

4.5 Continuous Time

The results of the first approach to simulating the model for continuous time in which seasonal lengths were exponentially distributed with parameter $\lambda = 1$ were not shown in this report. The reason is that the results were no different from those of discrete seasons. The only difference were the seasonal times, which were shorter in the continuous case than in the discrete case. The same difficulty that were encountered in the discrete case in regarding the late extinction time were also encountered in the continuous time.

However, due to limited time, we could not have a look at the second approach, where we planned approaching the continuous time model from a birth-death point of view.

5. Conclusion and Recommendations

We give our concluding remarks and recommendations for further work in this chapter.

5.1 Conclusion

The study revolved around a discrete time population-size-dependent binary-splitting process in which an individual at the end of one season either splits into two new individuals or just dies out. The probability of splitting into two depends on three factors namely, the carrying capacity of the habitat K, the current population size Z_n, and a scaling parameter v. The study considered two main cases. In the first case, we assumed that the carrying capacity was fixed and could take values such as 100, 1000, and 10000. The second case is where we allowed the carrying capacity to vary randomly in every season between $L = 100$ representing bad season, and $H = 1000$ representing good season, chosen randomly with equal probability.

In both cases, we were particularly interested in observing and recording two main properties of such a process. One of such properties is the expected time to extinction (late extinction in particular). We were also interested in estimating the probabilities of these two types of extinction occurring. The purpose was to compare these simulated results with what has been presumed by the theoretical work done in (Klebaner et al., 2011).

Our simulation results for the estimates for the probabilities of early extinctions in both cases were in perfect agreement with the theory. So by complementary argument, we can conclude for those of late extinction. On the other hand, our simulated results for the estimates of the expected time to late extinction were inconclusive for certain parameter values in both cases, especially when the carrying capacity K, and the scaling parameter v were large, i.e. $K = 1000, 10000$, and $v > .55$. This is because the time to extinction was extremely larger in most instances, and therefore very difficult to observe in our simulations. We were only able to observe late extinctions in the following scenarios: $K = 100$ for $v = 0.55, 0.6, 0.65, 0.7, 0.75$; $K = 1000$ for $v = 0.55$; and K random for $v = 0.55, 0.6, 0.65, 0.7$. The observations made from these results suggest that for both fixed K and random K, the expected time to extinction is likely to be exponentially long in K, but not in v. A more general upper bound for the expected time to extinction has been proposed to be e^{vK}. Elsewhere (see (Jagers, 2010)), it was asserted that the expected time to extinction for a population-size-dependent binary-splitting process behaves like $\mathcal{O}\left(Ce^{cK}\right)$ for some unknown constant C, and a parameter $c < v$. When we compare our results as shown in table 4.1 with this theoretical result, we can only conclude that the unknown constant C is likely to be a very small number compared to the carrying capacity of the habitat.

We also observed that in all given pair of parameter values, the noise (or fluctuation) in the evolution of the process seems to minimise as $K \to \infty$ and as $v \to 1$ in the case where K is large and fixed. This suggested that the fluctuations in the evolution of the process may have an effect on the chances of observing extinction — the risk of ultimate extinction. Using central limit theorem arguments, we were able to discuss the risk of extinction in terms of the standard deviation of a corresponding process for fixed K. We observed that the risk of extinction decreases for K very large irrespective of the value of v, and it is of the order $\mathcal{O}\left(\frac{1}{\sqrt{(2v-1)K}}\right)$.

Simulation was however very challenging, since the expected time to extinction for larger values of K and increasing values of v had extremely larger upper bounds, which meant we would have to wait for a very long time to be able to observe and record extinction events. This therefore limited the number of cases that we could consider. For $K = 100$, it was possible to observe both types of extinction for values of $v = 0.55, 0.6, 0.65, 0.7, 0.75$. However for values of $v > 0.75$, if the population does not die out early, it lingers and fluctuates around the critical size for a very long time. This therefore means that, the fact that the probability of late extinction is close to one does not necessary mean that we will be able to observe and record such events. For example we were able to record late extinction for values of $v = 0.55, 0.6, 0.65, 0.7$ for K random whereas in the case of $K = 1000$, we were only able to record late extinction for $v = 0.55$.

5.2 Recommendations

In order to paint a full picture of the expected time to ultimate extinction, we recommend that an algorithm be developed that can help simulate the current model better so that we can record ultimate extinction in all cases for all values of v and K. We further recommend that more theoretical work be done on the random carrying capacity case since currently there is no known theoretical foundation for such a case. More scenarios of the random carrying capacity can be explored than the simplest case considered in this work. It will be very interesting to find a similar upper bound for the expected time to extinction in the case of random carrying capacities.

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Edward Korveh, Gothenburg, June 2016.

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